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Microdistribution and feeding dynamics of *Coilia nasus* (Engraulidae) larvae and juveniles in relation to the estuarine turbidity maximum of the macrotidal Chikugo River estuary, Ariake Sea, Japan

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Running title. Early life history of *Coilia nasus* (Engraulidae)

ABSTRACT

To evaluate the nursery value of the estuarine turbidity maximum (ETM) for the anadromous engraulid fish *Coilia nasus*, physical and biological samples were collected along the macrotidal Chikugo River estuary, southwestern Japan, from June 2005 to January 2006. Generally, eggs were distributed upstream from the ETM, whereas larvae were distributed in the ETM. The first cohort was washed out of the estuary by a large flood in early July. The second cohort appeared after the flood, gradually extending its distributional area through the estuary and growing to 100 mm in standard length (SL) by December. Larvae and juveniles (20–100 mm SL) fed selectively on copepods, specifically large calanoid species, whereas more developed juveniles fed on mysids. Prey organisms in guts were significantly more abundant and present in greater weights in the ETM (salinity < 10) than in the lower estuary (salinity > 10). The better feeding conditions were primarily attributable to consistently high densities of two large calanoid species, *Sinocalanus sinensis* and *Pseudodiaptomus inopinus*, in the ETM. In contrast, the poor feeding conditions in the lower estuary were likely due to a seasonal decrease in copepod density and the dominance of small copepods such as *Oithona* spp. Given that better feeding conditions contribute positively to the growth and survival of larvae and juveniles, we conclude that the ETM has a significantly higher nursery value for *C. nasus* than other habitats in the Chikugo River estuary.

Key words: anadromous fish, Ariake Sea, Chikugo River, *Coilia nasus*, copepod, estuarine turbidity maximum, selective feeding, nursery

INTRODUCTION

Although estuaries generally support high productivity in coastal waters, physical and biological conditions vary drastically even within an estuary. In addition to spatial variations, estuarine conditions fluctuate temporally with the tidal rhythm, freshwater discharge, and seasonal succession. In macrotidal estuaries, the hydrodynamic function of tidal pumping and estuarine circulation maintains high concentrations of suspended solids, forming an estuarine turbidity maximum (ETM) at low salinities (Allen *et al.*, 1980; Uncles *et al.*, 2002). Given that high densities of zooplankton are often associated with the ETM, many studies have suggested that growth and survival of larval and juvenile fish are higher in the ETM than in other areas due to its better feeding conditions (e.g., Dauvin and Dodson, 1990; Martino and Houde, 2010; North and Houde, 2003; Shoji *et al.*, 2005; Sirois and Dodson, 2000). Despite the growing understanding of the nursery value of the ETM, intensive sampling in the ETM has been conducted only in spring and summer when larval and juvenile fish are abundant. Year-round assessment is, therefore, essential to improving our understanding of the nursery value of the ETM in relation to the spatiotemporal dynamics of estuarine conditions.

Coilia nasus is an engraulid fish endemic to the innermost part of the Ariake Sea, Japan (Takita, 1967a, 1978; Yamada *et al.*, 2007). This species is important to local fisheries and is defined as an anadromous fish (Takita, 1967b). Congenerous species have a wide distribution in lacustrine, riverine, estuarine, and coastal waters in East Asia (Whitehead *et al.*, 1988). Ecological information about *C. nasus* has been accumulated mainly in the macrotidal Chikugo River estuary, which is the largest estuary flowing into the Ariake Sea. Adults migrate to the tidal freshwater area (> 15 km upstream from

66 the sea) to spawn pelagic eggs in summer (Matsui *et al.*, 1986a; Ohmura *et al.*, 2012;
67 Takita, 1967b). Eggs and larvae show high survival rates only at salinities < 10
68 (Fukunaga and Hamasaki, 1998; Matsui *et al.*, 1986b). Larvae and juveniles feed
69 primarily on cladocerans and copepods, gradually extending their distributional area to
70 the sea (Matsui *et al.*, 1987). Although such ecological characteristics suggest a great
71 dependence of *C. nasus* on the estuary, few studies have addressed the feeding, growth,
72 and survival of *C. nasus* larvae and juveniles in relation to the unique macrotidal
73 environment, specifically the well-developed ETM (cf., Suzuki *et al.*, 2012a).
74 In the macrotidal Chikugo River estuary, the ETM develops at salinities < 10
75 especially during spring tides under usual freshwater discharge levels (Suzuki *et al.*,
76 2007, 2009a). A large biomass of copepods is present in the ETM throughout the year
77 (Suzuki *et al.*, 2013). In contrast, copepod biomass is usually smaller and seasonally
78 variable in areas outside the ETM (Suzuki *et al.*, 2013). Furthermore, mysid biomass is
79 larger in the ETM than outside the ETM (Suzuki *et al.*, 2009b). We hypothesize that *C.*
80 *nasus* larvae and juveniles benefit from the better feeding conditions in the ETM
81 irrespective of the season. To test this hypothesis, we examine the feeding dynamics of
82 *C. nasus* larvae and juveniles from the first feeding to the first overwintering. Physical
83 and biological samples were collected along the Chikugo River estuary from June 2005
84 to January 2006. Gut contents of *C. nasus* larvae and juveniles were analyzed in relation
85 to zooplankton composition in the environment. Our discussion focuses on contrasting
86 the nursery value of the ETM with that of the lower estuary.
87

MATERIALS AND METHODS

Study area

The Chikugo River estuary is the largest estuary in the Ariake Sea in terms of both catchment area (2860 km^2) and freshwater discharge (annual median of daily averages: 60 m^3 s^{-1}). The estuarine environment is characterized by one of the largest tidal ranges in Japan (up to 5 m during spring tides). The tidal reach extends to the Chikugo Weir 23 km upstream from the river mouth (Fig. 1). Strong tidal currents completely mix the water column during spring tides, whereas partial stratification occurs during neap tides (Suzuki *et al.*, 2007). The ETM is usually located 10–20 km upstream from the river mouth at spring high tide, although it is transported back and forth over a 20-km range along the estuary with the semidiurnal tidal cycle between high and low tides. The copepod community of the ETM is overwhelmingly dominated by *Sinocalanus sinensis*, except in summer when *Pseudodiaptomus inopinus* outnumbers *S. sinensis* (Suzuki *et al.*, 2013). The mysid *Hyperacanthomysis longirostris* maintains dominance in and close to the ETM throughout the year (Suzuki *et al.*, 2009b). A description of the dynamics of particulate organic matter in the Chikugo River estuary is published elsewhere (Suzuki *et al.*, 2007, 2009a, 2012a). Overall, physical and biological conditions change clearly with the salinity gradient along the Chikugo River estuary. In the present study, salinity was used to separate the ETM (salinity < 10) from the lower estuary (salinity >10). As *C. nasus* larvae and juveniles are distributed exclusively in the ETM and the lower estuary (Matsui *et al.*, 1987; Takita, 1967b), the tidal freshwater area, which was included in the ETM for convenience, had little influence on comparisons between the ETM and the lower estuary.

Seven regular sampling stations (R1–R7; Fig. 1) were set up at intervals of

112 1.5–5.5 km along the lower reaches of the Chikugo River; they were located between
113 the river mouth and the upper limit of the tidal reach (23 km upstream). Three regular
114 sampling stations (E1–E3; Fig. 1) were set up along the main tidal channel of the river
115 so that E1 was near the river mouth and E3 was at the edge of the tidal flat (9 km
116 offshore). Three extra sampling stations (R2.5, R3.5, and R6.5; Fig. 1) were set up in or
117 close to the spawning area of *C. nasus*. The freshwater discharge was continuously
118 monitored 26 km upstream and the data were uploaded to the web site
119 (http://www.qsr.mlit.go.jp/chikugo/data/09-sokuhou/index.html) by the Chikugogawa
120 River Office. For tidal ranges, water level differences were calculated between low and
121 high tides in the morning using values that had been predicted for Ohmuta (16 km south
122 of the river mouth) by the Japan Meteorological Agency (2004).
123
124 *Field sampling*
125 Three sampling methods were used to collect *C. nasus* eggs, larvae, and juveniles (Fig.
126 2). In *C. nasus*, the transition between the larval and juvenile stages occurs at ca. 30 mm
127 in standard length (ca. 35 mm in total length; Takita, 1967b). For eggs and larvae, a
128 small ring net (45 cm mouth diameter, 0.33 mm mesh aperture along the 200 cm conical
129 body) was towed in the surface water by a boat for 3–10 min at approximately 1 m s^{-1}
130 against the water currents. The sampling was conducted in or close to the spawning area
131 of *C. nasus* in the upper estuary (R2.5–R7 including extra stations) 14 times between 8
132 June and 23 August in 2005. For more developed larvae and juveniles, a large ring net
133 (130 cm mouth diameter, 1 mm mesh aperture along the 350 cm cylindrical body and
134 0.33 mm mesh aperture at the 150 cm conical end) was towed as described above.
135 Sampling was conducted at the 10 regular stations (R1–R7, E1–E3) during spring tides

136 monthly between August and October 2005. Catches from the small and large ring nets
137 were preserved in 99% ethanol. The sampling was always started at the uppermost
138 station (R7) and finished at the lowermost station (R2.5 or E3) within 4–5 h around high
139 tide in the morning. At each station, zooplankton were sampled by towing a plankton
140 net (45 cm mouth diameter, 0.1 mm mesh aperture along the 100 cm conical body)
141 vertically from the bottom to the surface. Catches from the plankton net were preserved
142 in 5% formalin seawater solution. The volume of water filtered through each net was
143 calculated using digital flow meters that were attached to the respective mouths of the
144 nets. Temperature, salinity, and turbidity were measured in the surface water using an
145 environmental monitoring system (6920 Sonde and 650 MDS Display, YSI, Yellow
146 Springs, Ohio, USA).

147 Finally, to sample more developed juveniles, Shige-ami fishing (a traditional
148 fishing method used in the Ariake Sea) was conducted at R4 and E1 during spring tides
149 monthly between October 2005 and January 2006. This method of fishing collects fish
150 using a net fixed to the bow of an anchored boat. Fish that swim with water currents are
151 efficiently trapped in the net, especially during the ebb tide. Trapped *C. nasus* juveniles
152 were sampled at 5 min intervals using a dip net and frozen onboard. The frozen
153 specimens were thawed and then preserved in 99% ethanol in the laboratory.
154 Temperature, salinity, and turbidity were measured in the surface water every 10 min.
155 Because the fishing was conducted for 2 h at each station during the ebb tide, salinity
156 decreased with time. This allowed sampling of *C. nasus* from a relatively wide salinity
157 range (usually 5–25 at E1).

158

159 *Laboratory analysis*

160 Eggs, larvae, and juveniles of *C. nasus* were enumerated for samples from each station
161 on each sampling date. The standard length (SL) of all specimens was measured, with
162 the exception of random selection of specimens at stations where the number of
163 specimens far exceeded 100. To obtain a SL frequency distribution for each sampling
164 date, SL frequency distributions at all stations were accumulated after weighted in
165 proportion to the density of *C. nasus* at each station. Comparisons of SL frequency
166 distributions between the three sampling methods revealed a strong bias toward small
167 individuals in samples from the small ring net on 23 August and from the large ring net
168 on 17 October. To minimize the possibility of net avoidance by larger individuals, these
169 samples were not used for further analysis. Sample shrinkage incidental to preservation
170 in ethanol was not considered.

171 When available, approximately 20 *C. nasus* individuals (larvae and/or
172 juveniles) were randomly picked for each station on each sampling date after 24 July,
173 since when a single large cohort of *C. nasus* occurred continuously (see Results). Under
174 a stereomicroscope, gut contents were removed from the stomach and intestine of larvae
175 and from the stomach of juveniles. Gut contents were enumerated and identified to the
176 lowest taxonomic level possible. Using diagnostic characters (Chihara and Murano,
177 1997; Mizuno and Takahashi, 2000; Shen and Mizuno, 1984), copepods and mysids
178 were identified to species or genera and other prey organisms to orders or classes. To
179 calculate dry weights, body lengths of the four dominant prey taxa Rotifera, Cladocera,
180 Copepoda, and Mysidacea (see Results) were measured using an eyepiece graticule in
181 the stereomicroscope. The body lengths were converted into dry weights using
182 length-weight relationships devised by Uye (1982) and Pauli (1989).

183 Zooplankton samples from the environment were processed in the same way as

184 gut contents. To show spatial patterns of occurrence of dominant zooplankton taxa along
185 the salinity gradient of the Chikugo River estuary, monthly zooplankton data from June
186 2005 to January 2006 were used (cf., Suzuki *et al.*, 2013). In the present study, the 0.1
187 mm mesh was used for the plankton net to achieve the maximum sampling efficiency in
188 turbid waters. Although this mesh size is considered fine enough to catch the majority of
189 potential food taxa for *C. nasus*, the density of small zooplankton, such as rotifers and
190 copepod nauplii, might have been underestimated. Given strong vertical mixing in the
191 Chikugo River estuary especially during spring tides (Suzuki *et al.*, 2007, 2009a, 2012a),
192 zooplankton samples obtained from the water column were considered to represent food
193 availability for *C. nasus*.

194 To evaluate the food preference of *C. nasus* at each station on each sampling
195 date, an electivity index (E_i*, Vanderploeg and Scavia, 1979) was calculated as follows:

196 $$E_i^* = [W_i - (1/N)]/[W_i + (1/N)] \quad (1)$$

197 $$W_i = (r_i/p_i)/[\Sigma(r_i/p_i)] \quad (2)$$

198 where r_i and p_i represent the relative abundance of food types in the gut and the
199 environment, respectively. The number of food types is designated by N. The electivity
200 index E_i* changes between plus and minus one with zero indicating random feeding.
201 Although the use of E_i* is recommended for evaluating food preferences, the maximum
202 preference value (E_i* = 1) can be attained only under these unrealistic conditions: $r_i = 1$,
203 $p_i = 0$, and $N = \infty$ (Lechowicz, 1982). It is also important to note that the maximum
204 attainable preference value increases with N. In the present study, E_i* was calculated for
205 the above-mentioned four dominant prey taxa. It was also calculated for the six
206 dominant copepod categories *S. sinensis*, *P. inopinus*, *Acartia* spp., *Parvocalanus*
207 *crassirostiris*, *Oithona* spp., and all copepod nauplii. Ontogenetic changes in the food

208 preference of *C. nasus* were examined using E_i* and mean SL at each station on each
209 sampling date.
210

211 **RESULTS**

212 *Spatiotemporal occurrence of Coilia nasus*

213 In summer 2005, the daily freshwater discharge remained < 100 $m^3 s^{-1}$ until June, with a
214 minimum of < 20 $m^3 s^{-1}$ from 17 to 25 June (Fig. 3a). The discharge increased in early
215 July, causing a large flood event from 9 to 14 July with a peak of 1768 $m^3 s^{-1}$ on 11 July.
216 Following this flood, the discharge returned to < 100 $m^3 s^{-1}$ by late July. Surface water
217 temperature increased gradually from 24 to 28°C before dropping to < 25°C during the
218 flood period (Fig. 3b). Higher temperatures of 25–31°C occurred continuously after the
219 flood period. Surface water turbidity changed clearly with the fortnightly tidal cycle,
220 although it dropped to < 50 NTU (nephelometric turbidity unit) after the flood period
221 (Fig. 3c). Turbidity peaks were found more upstream during spring tides than during
222 neap tides, exceeding 200 NTU at salinity 1. *Coilia nasus* eggs always showed higher
223 densities (> 10 eggs m^{-3}) immediately after neap tides, even during the flood period (Fig.
224 3d). In contrast, the density of *C. nasus* larvae did not vary with the fortnightly tidal
225 cycle (Fig. 3e). Although larvae disappeared during the flood period, they reached a
226 maximum density of 600 ind m^{-3} afterward. As for spatial distribution, larvae showed
227 density peaks at salinity 1, whereas eggs were always distributed more upstream
228 (salinity < 1).

229 Two distinct cohorts of *C. nasus* were found in the series of SL frequency
230 distributions of specimens sampled using the small ring net (Fig. 4). The first cohort
231 appeared in early June and increased in mean SL from 5.3 mm on 8 June to 18.3 mm on
232 4 July. This cohort, however, disappeared during the flood period of early July. The
233 second cohort appeared after the flood period and increased in mean SL from 3.3 mm
234 on 19 July to 20.7 mm on 9 August. The second cohort appeared successively in the

series of unimodal SL frequency distributions of specimens sampled using the large ring net and Shige-ami fishing (Fig. 5). The monthly mean SL of specimens sampled over the whole estuary were 31, 44, 72, 88, and 102 mm from August to December in 2005 but remained at 100 mm until January 2006. As for spatial distribution, larvae and juveniles concentrated in the ETM (salinity < 10) in August, whereas in September they were distributed throughout the estuary. Although the density of juveniles could not be determined from the non-quantitative Shige-ami fishing samples, the majority of specimens were sampled in the ETM (except in December). However, significantly larger specimens (Mann-Whitney test, $P < 0.05$) were always found in the lower estuary (salinity > 10), with the monthly mean SLs of 40, 52, 104, 106, 105, and 111 mm from August to January.

Feeding dynamics of Coilia nasus

A typical pattern of the feeding dynamics of *C. nasus* was observed in September when larvae and juveniles occurred at all stations except the uppermost R7. A maximum *C. nasus* density of 0.6 ind m^{-3} was found in the ETM, where surface water salinity and turbidity were 0.8 and 481 NTU, respectively (Fig. 6a, b). In the environment, copepods dominated numerically throughout the estuary, except at R7 where rotifers outnumbered copepods (Fig. 6c). The density of copepods showed a bimodal pattern along the estuary, exceeding 50 ind L^{-1} at R4, R5, and E3. Copepods accounted for > 95% by number of the gut contents of *C. nasus* at each station (Fig. 6d). The number of gut contents per fish was larger in the ETM than in the lower estuary, even though the SL of *C. nasus* was smaller in the ETM than in the lower estuary (Fig. 6b). Comparisons of the copepod category composition between the environment and gut contents indicated that

259 *C. nasus* preferred large copepods such as *P. inopinus* (E_i* = 0.4 to 0.7) over small
260 copepods such as *Oithona* spp. (E_i* = -1.0 to -0.9) and nauplii (E_i* = -1.0 to 0). Among
261 dominant prey taxa excluding copepods, *C. nasus* clearly preferred cladocerans and
262 mysids over rotifers.

263 The physical and biological environment during spring tides formed similar
264 longitudinal profiles along the estuarine salinity gradient from June 2005 to January
265 2006. Surface water turbidity exceeded 100 NTU at salinities 0.1–10, with highest
266 values at salinity 1 (Fig. 7a). Rotifers and cladocerans concentrated at salinities < 1,
267 whereas mysids occurred primarily at salinities > 1 (Fig. 7b). The density of copepods
268 always exceeded 1 ind L^{-1} at salinities 0.1–10, although it often dropped to 0.1 ind L^{-1}
269 outside this salinity range, especially in the cold season. The dominant oligohaline
270 copepods *S. sinensis* and *P. inopinus* were wholly responsible for the high copepod
271 densities observed at salinities 0.1–10 (Fig. 7c). In contrast, the dominant
272 meso/polyhaline copepods *Acartia* spp., *Parvocalanus crassirostris*, and *Oithona* spp.
273 usually concentrated at salinities > 10. Copepod nauplii occurred throughout the estuary,
274 exhibiting higher densities at salinities 0.1–10.

275 The electivity index E_i* revealed ontogenetic changes in the food preference of
276 *C. nasus*. Among the four dominant prey taxa, cladocerans were highly selected by *C.*
277 *nasus* in the SL range of < 60 mm, whereas copepods were generally selected by *C.*
278 *nasus* in the SL range of 20–100 mm (Fig. 8a). *Coilia nasus* switched its diet from
279 copepods to mysids at 100 mm SL. In contrast, rotifers were usually avoided, even by
280 small larvae (< 20 mm SL). Among dominant copepod categories, the two large
281 copepods *S. sinensis* and *P. inopinus* were selected irrespective of the SL of *C. nasus*
282 (Fig. 8b). In contrast, nauplii and the small copepod *Oithona* spp. were not selected at

283 all, except by *C. nasus* of < 10 mm SL, which selected nauplii.

284 The number of prey organisms in the guts of each *C. nasus* was larger in the
285 ETM than in the lower estuary (Fig. 9a), although copepods overwhelmingly dominated
286 the gut contents in both habitats (Fig. 9b, c). Significantly larger numbers of prey
287 organisms were found in the ETM in *C. nasus* SL classes of 50–60, 60–80, 80–100 and
288 > 100 mm (Mann-Whitney test, $P < 0.05$). Prey organisms were always dominated by
289 the two large copepods *S. sinensis* and *P. inopinus* in the ETM, whereas small copepods
290 such as *Oithona* spp. dominated in the lower estuary. Individual dry weights were > 10
291 times greater for *S. sinensis* and *P. inopinus* compared with *Oithona* spp. As a result, the
292 weight of prey organisms in the guts of each *C. nasus* was greater in the ETM than in
293 the lower estuary (Fig. 10a). Significantly greater weights of prey organisms were found
294 in the ETM in *C. nasus* SL classes of 40–50, 50–60, 60–80, and 80–100 mm
295 (Mann-Whitney test, $P < 0.05$). The two large copepods *S. sinensis* and *P. inopinus*
296 overwhelmingly dominated the gut contents by weight in the ETM (Fig. 10b, c).
297 Although small copepods dominated the gut contents by weight in the lower estuary,
298 mysids outweighed copepods in the *C. nasus* SL classes of > 80 mm.
299

DISCUSSION

Spatiotemporal occurrence of Coilia nasus

In contrast to other anadromous fish that spawn pelagic eggs for a short period of time (e.g., American shad, Williams and Daborn, 1984; Striped bass, Secor and Houde, 1995), reproduction of *C. nasus* is characterized by a long spawning season ranging from May to August (Matsui *et al.*, 1986a; Takita, 1967b). In summer 2005, higher densities of *C. nasus* eggs were observed repeatedly after neap tides irrespective of drastic changes in freshwater discharge and temperature (Fig. 3). This finding agrees closely with previous reports that the spawning migration of *C. nasus* increases during the neap-spring transition period (Matsui *et al.*, 1986a; Ohmura *et al.*, 2012; Yoshimoto and Kitajima, 1993). Given that the density of copepods generally increases in the Chikugo River estuary during the neap-spring transition period (Suzuki *et al.*, 2012b), newly hatched larvae may be favored by better feeding conditions at this time. In contrast with *C. nasus*, temperature is a prime determinant of the intensive spawning of American shad (Williams and Daborn, 1984) and striped bass (Secor and Houde, 1995). Although the ecological significance of the fortnightly spawning cycle of *C. nasus* remains to be studied, it may prove to be a unique strategy for spreading the risk of reproduction failures through its long spawning season.

The spatiotemporal occurrence of eggs and larvae combined with the succession of the SL frequency distribution clearly illustrated the disappearance of the first cohort in the year class of 2005 (Figs. 3, 4). As pelagic eggs of *C. nasus* hatch 19–21 h after fertilization at temperatures of 24–26°C (Takita, 1967b), eggs and newly hatched larvae can remain within the tidal reach under usual freshwater discharge levels (Hayashi *et al.*, 1994; Matsui *et al.*, 1986b). However, the first cohort was probably

washed out of the estuary by the large flood that occurred in early July. High salinities would have caused substantial mortality in the sea, as *C. nasus* eggs and larvae are highly vulnerable to salinities > 10 (Fukunaga and Hamasaki, 1998; Matsui *et al.*, 1986b). In addition, the first cohort possibly suffered from deteriorated feeding conditions during the flood period when copepods almost completely disappeared from the estuary (Suzuki *et al.*, 2012b). The second cohort appeared after the flood period and constituted the majority of the year class (Figs. 4, 5). Having grown to the juvenile stage (> 30 mm SL), the second cohort survived a large flood in early September (Fig. 2). This indicates that the second cohort had already have gained tolerance to variations in salinity, food availability, and water currents. The SL frequency distributions of the second cohort continuously shifted to larger sizes until reaching a ceiling of 100 mm SL in December. In addition, larger specimens were always sampled in the lower estuary in each month. Although more developed juveniles likely extended their distributional area downstream, they remained in the estuary until they grew to 100 mm SL. Previous studies have suggested that *C. nasus* juveniles begin migration to the sea at a size of 100 mm SL in October at the earliest (Hayashi *et al.*, 2002; Ishida, 1990; Matsui *et al.*, 1987). Overall, prolonged inhabitation in the estuary is considered to be an essential component in the early life history of *C. nasus*.

Feeding dynamics of Coilia nasus

Ontogenetic changes in the food preference of *C. nasus* were confirmed over a wide range of SLs (Figs. 6, 8): cladocerans (< 60 mm SL), copepods (20–100 mm SL), and mysids (> 100 mm SL). In general, food preferences for crustacean zooplankton are considered common among species in the genus *Coilia* (Chen and Zhu, 2008; Varghese,

348 1961). The present study is the first to document that *C. nasus* prefers mysids, whereas
349 our other results agree exactly with Matsui *et al.* (1987). However, the preference for
350 cladocerans is still uncertain, as cladocerans are less able to escape planktivorous fish
351 than copepods (Drenner *et al.*, 1978). Our further analysis revealed that *C. nasus*
352 selected larger species from copepod communities in the environment, as has been
353 reported for other fishes in estuaries (e.g., Hibino *et al.*, 1999; Islam *et al.*, 2006a, b;
354 Robichaud-LeBlanc *et al.*, 1997). Despite the general categorization of engraulid fishes
355 as filter feeders, anchovies switch their feeding behavior from filtering to biting in
356 response to environmental conditions (James and Findlay, 1989; Leong and O'Connell,
357 1969). *Coilia nasus* would improve its foraging efficiency (i.e., energy gain per unit
358 foraging effort) by feeding on larger copepods, although the mechanism of the selective
359 feeding by *C. nasus* remains to be studied.

360 Significantly better feeding conditions for *C. nasus* in the ETM were
361 demonstrated by comparing both number and weight of prey organisms in guts between
362 the ETM and the lower estuary (Figs. 9, 10). Previous studies have reported similar
363 spatial differences in gut contents of other larval and juvenile fishes along the Chikugo
364 River estuary (Hibino *et al.*, 1999; Islam *et al.*, 2006a, b; Suzuki *et al.*, 2008). The better
365 feeding conditions observed in the ETM are primarily attributable to consistently high
366 densities of the two large oligohaline copepods *S. sinensis* and *P. inopinus* (Fig. 7).
367 Moreover, the ETM is considered advantageous for planktivorous fish because high
368 turbidity has less influence on the foraging efficiency of planktivorous fish than on that
369 of piscivorous fish (i.e., predators of planktivorous fish; De Robertis *et al.*, 2003). In
370 contrast, the poor feeding conditions observed in the lower estuary were likely due to a
371 seasonal decrease in copepod density and the dominance of small copepods such as

372 *Oithona* spp. (Suzuki *et al.*, 2013). Generally, better feeding conditions for larval and
373 juvenile fish in the ETM are considered common in many estuaries (e.g., St. Lawrence
374 River, Dauvin and Dodson, 1990; Sirois and Dodson, 2000; Chesapeake Bay, Martino
375 and Houde, 2010; North and Houde, 2003; Shoji *et al.*, 2005). Nevertheless, it is notable
376 that *C. nasus* takes advantage of the ETM continuously from summer to winter;
377 previous studies have usually addressed the feeding dynamics of larval and juvenile fish
378 in spring and summer only. Although some *C. nasus* juveniles migrate offshore to
379 overwinter at higher water temperatures (cf., Hibino *et al.*, 2007), others may stay in the
380 ETM to benefit from better feeding conditions, even in winter.
381
382 *Implications for the* Coilia nasus *population*
383 The present study demonstrated the great dependence of *C. nasus* larvae and juveniles
384 on the ETM (Fig. 11). Eggs are spawned in the tidal freshwater area, whereas newly
385 hatched larvae are distributed in the ETM. During the long spawning season, large
386 floods occasionally strike the estuary. Given the vulnerability of eggs and larvae to high
387 salinities (Fukunaga and Hamasaki, 1998; Matsui *et al.*, 1986b), they usually do not
388 survive far downstream from the ETM. Even after acquiring physiological tolerance,
389 juveniles likely stay in the ETM to utilize the high densities of large copepods.
390 Moreover the dominant mysid *H. longirostris* occurs abundantly in and close to the
391 ETM (Suzuki *et al.*, 2009b), assuring better feeding conditions for more developed
392 juveniles. Such better feeding conditions in the ETM will contribute positively to the
393 growth and survival of *C. nasus* from the first feeding to the first overwintering. In
394 addition, potential predators are considered less abundant in the ETM than in the lower
395 estuary (Shoji *et al.*, 2006). Assessment of growth and survival of *C. nasus* larvae and

juveniles in each habitat is the next issue that needs to be studied. Although direct evaluation of the contribution of each habitat to adult recruitment is necessary to identify a nursery (cf. Beck *et al.*, 2001), our overall results indicate that the ETM holds significantly higher nursery value for *C. nasus* than other habitats in the Chikugo River estuary.

Coilia nasus is one of seven continental relict fishes occurring only in the Ariake Sea within Japan (Sato and Takita, 2000). Macrotidal estuaries characteristic of the innermost part of the Ariake Sea are thought to be primarily responsible for the survival of the relict fish populations after the isolation of the Japanese Archipelago from the Eurasian Continent by marine transgressions (Hibino *et al.*, 2002; Sato and Takita, 2000; Yagi *et al.*, 2011). Reproduction of the relict *C. nasus* population depends greatly on the Chikugo River estuary (Matsui *et al.*, 1986b; Takita, 1967b), although sporadic reproduction has been observed in other estuaries of the Ariake Sea (Igita, 1986; Yagi *et al.*, 2011). Given high fishing pressure on migrating adults during the spawning season (Takita, 1967b; Yoshimoto and Kitajima, 1993), effective fishing regulations are necessary to preserve the relict *C. nasus* population. The present study indicates that a temporary prohibition of fishing following large floods will facilitate the occurrence of large cohorts that should constitute the majority of the year class of *C. nasus*. Furthermore, conservation of the unique macrotidal estuarine environment will be important to preserve all of the relict fishes, including *C. nasus*.

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598

599 **FIGURE LEGENDS**

600 **Figure 1.** Study areas and sampling stations along the Chikugo River estuary on the
601 Kyushu Island in southwestern Japan. Filled and open circles represent our regular
602 and extra sampling stations, respectively. The Chikugo Weir is represented by a filled
603 rectangle. Filled and open triangles represent observation points for freshwater
604 discharges and tidal ranges, respectively.

605 **Figure 2.** Interrelations among seasonal changes in freshwater discharge and
606 temperature (a), the temporal occurrence of *Coilia nasus* (b), and schedules of
607 sampling (c) in the Chikugo River estuary from February 2005 to January 2006.
608 Monthly temperature consists of both mean (horizontal line) and range (vertical line)
609 observed in the surface water through the estuary under a monthly sampling program
610 (Suzuki *et al.*, 2012a). Filled triangles represent applications of each sampling
611 method.

612 **Figure 3.** Interrelations among daily fluctuations in freshwater discharge and tidal range
613 (a), and spatiotemporal changes in temperature (b), turbidity (c), and the density of
614 *Coilia nasus* eggs (d) and larvae (e) observed in the surface water along the upper
615 Chikugo River estuary from 8 June to 9 August in 2005. Sampling dates are
616 represented by filled circles in the tidal range plot. The isopleth charts are overlaid
617 with salinity contour lines. Filled triangles represent the locations of the sampling
618 stations. Up- and downward arrows represent the middle of spring and neap tides,
619 respectively.

620 **Figure 4.** Frequency distributions of the standard length of *Coilia nasus* representing
621 each sampling date from 8 June to 9 August in 2005. All specimens were sampled in
622 the estuarine turbidity maximum (salinity <10) using a small ring net (45 cm mouth

623 diameter, 0.33 mm mesh aperture along the 200 cm conical body). The mean standard
624 length and the number of specimens analyzed are represented by M and *N*,
625 respectively.

626 **Figure 5.** Monthly frequency distributions of the standard length of *Coilia nasus* from
627 August 2005 to January 2006. Filled and open bars represent specimens sampled in
628 the estuarine turbidity maximum (ETM, salinity < 10) and the lower estuary (salinity
629 > 10), respectively. Sampling was conducted using a large ring net (130 cm mouth
630 diameter, 1 mm mesh aperture along the 350 cm cylindrical body and 0.33 mm mesh
631 aperture at the 150 cm conical end) in August and September, and Shige-ami fishing
632 from October to January. The mean standard length and the number of specimens
633 analyzed are represented by M and *N*, respectively. Information about specimens
634 sampled in the whole and lower estuary is shown on the left and right sides of each
635 monthly chart, respectively. Monthly charts are partially magnified in October and
636 November.

637 **Figure 6.** Interrelations among the physical environment (a; salinity and turbidity), the
638 occurrence of *Coilia nasus* (b; density and frequency distributions of standard length),
639 zooplankton densities in the environment (c), and prey organisms in the guts of *C.*
640 *nasus* (d) observed at the ten regular sampling stations along the Chikugo River
641 estuary on 19 September in 2005. Major zooplankton categories are represented by
642 different patterns in the bar charts.

643 **Figure 7.** Turbidity (a), the density of dominant prey taxa (b), and the density of
644 dominant copepod categories (c) observed along the salinity gradient of the Chikugo
645 River estuary monthly from June 2005 to January 2006 (cf., Suzuki *et al.*, 2013).
646 Note that all axes are transformed logarithmically.

647 **Figure 8.** The electivity index (E_i*, Vanderploeg and Scavia, 1979) of *Coilia nasus* for
648 dominant prey taxa (a) and dominant copepod categories (b) in relation to the mean
649 standard length of *C. nasus*. Each symbol represents E_i* observed at each station in
650 the Chikugo River estuary from 24 July in 2005 to 16 January in 2006.
651 **Figure 9.** The number of prey organisms in the guts of *Coilia nasus* in relation to
652 standard length (a), accompanied by the numerical composition of prey organisms
653 observed in the estuarine turbidity maximum (b; ETM, salinity < 10) and the lower
654 estuary (c; salinity > 10). Each symbol represents individual specimens sampled in
655 the Chikugo river estuary from 24 July in 2005 to 16 January in 2006. The two large
656 copepods *Sinocalanus sinensis* and *Pseudodiaptomus inopinus* constitute Copepoda
657 (large), whereas Copepoda (others) consists mainly of small copepods and
658 unidentified copepods. The number of specimens analyzed is represented by *N*.
659 **Figure 10.** The weight of prey organisms in the guts of *Coilia nasus* in relation to
660 standard length (a), accompanied by the weight composition of prey organisms
661 observed in the estuarine turbidity maximum (b; ETM, salinity < 10) and the lower
662 estuary (c; salinity > 10). See Fig. 8 for details.
663 **Figure 11.** The early life history of the anadromous engraulid fish *Coilia nasus* in the
664 macrotidal Chikugo River estuary. Adults spawn pelagic eggs in the tidal freshwater
665 area in summer. Larvae are distributed in the estuarine turbidity maximum (ETM,
666 salinity < 10) under usual freshwater discharge levels, whereas they are highly
667 vulnerable to large floods. Although juveniles extend their distributional area through
668 the estuary, they benefit from better feeding conditions only in the ETM where large
669 copepods occur abundantly. Some juveniles migrate offshore to overwinter at higher
670 water temperatures, whereas others stay in the ETM even in winter under the better

671 feeding conditions.

Fig. 1

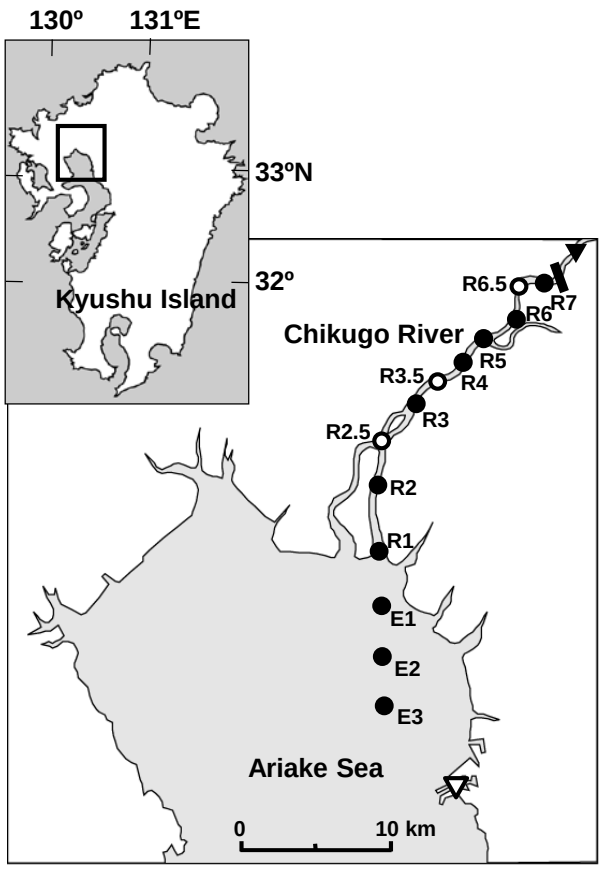
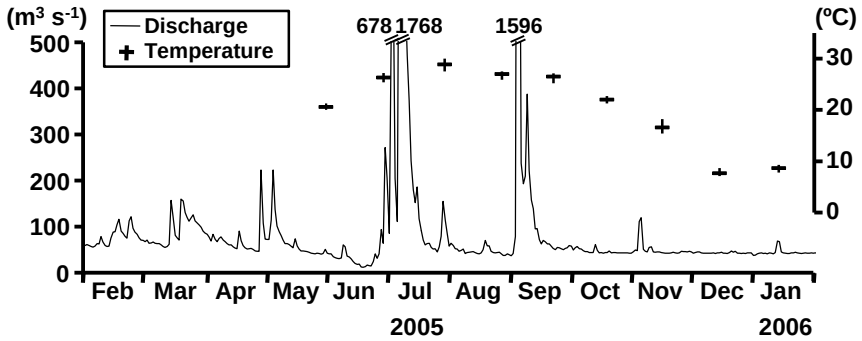
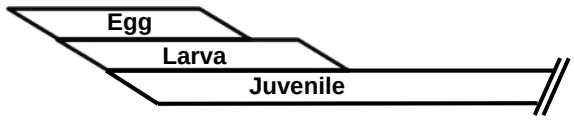

130º
131ºE
33ºN
32º
Kyushu Island
Chikugo River
R6.5
R7
R6
R5
R3.5
R4
R3
R2.5
R2
R1
E1
E2
E3
Ariake Sea
0
10 km

Fig. 2

(a) Discharge and Temperature



(b) Temporal occurrence of *Coilia nasus*



(c) Schedules of sampling

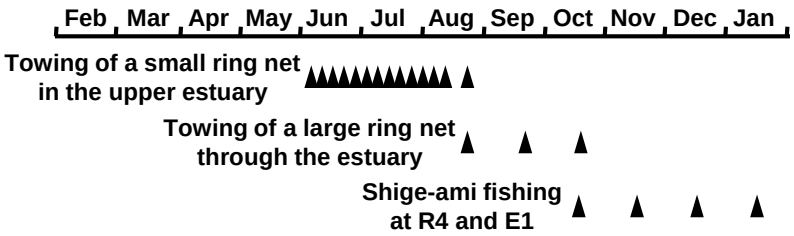


Fig. 3

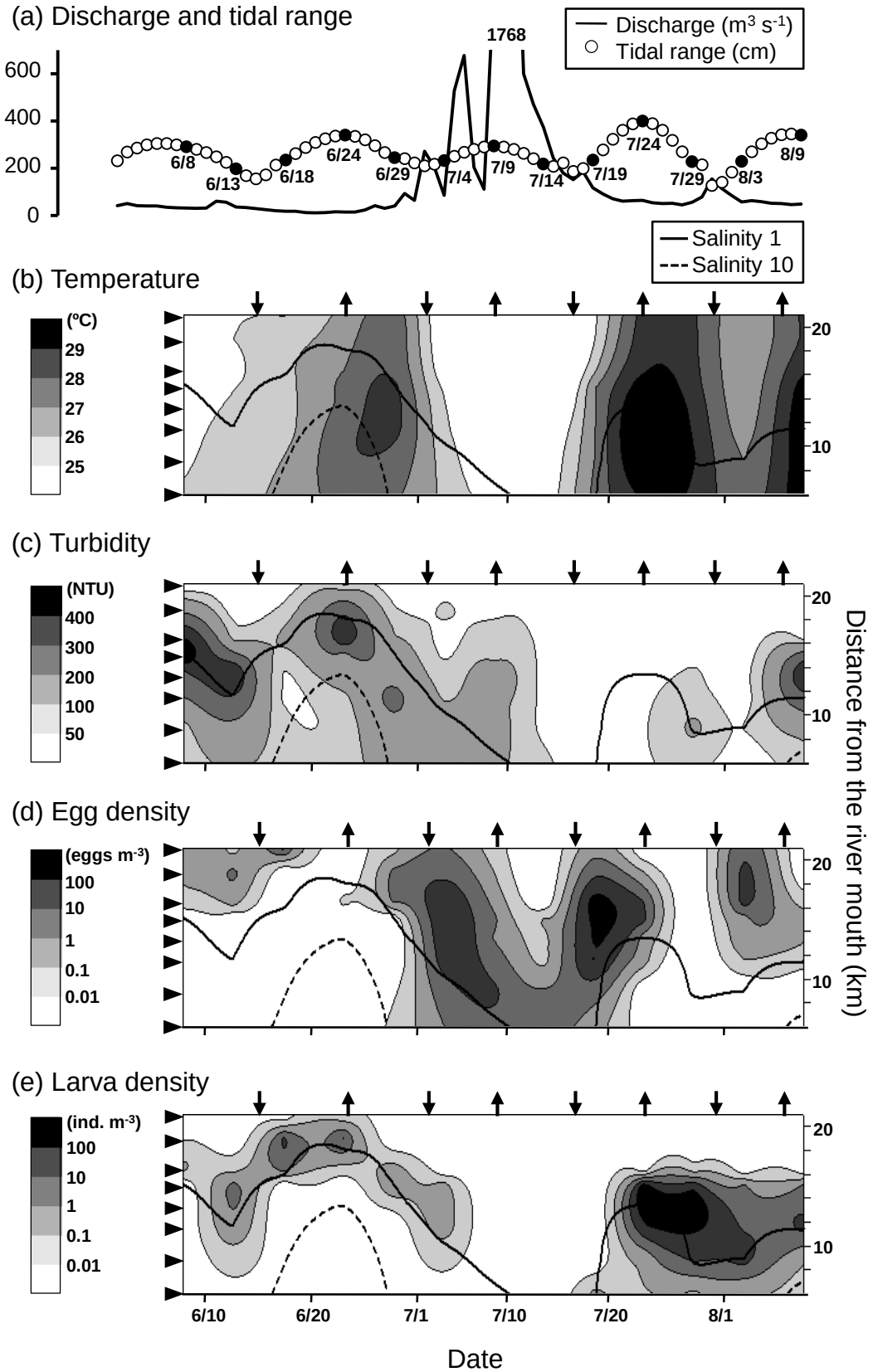

(a) Discharge and tidal range
Discharge (m3 s-1)
Tidal range (cm)
1768
600
400
200
0
6/8
6/13
6/18
6/24
6/29
7/4
7/9
7/14
7/19
7/24
7/29
8/3
8/9
Salinity 1
Salinity 10
(b) Temperature
(ºC)
29
28
27
26
25
(c) Turbidity
(NTU)
400
300
200
100
50
(d) Egg density
(eggs m-3)
100
10
1
0.1
0.01
(e) Larva density
(ind. m-3)
100
10
1
0.1
0.01
20
10
Distance from the river mouth (km)
6/10
6/20
7/1
7/10
7/20
8/1
Date

Fig. 4

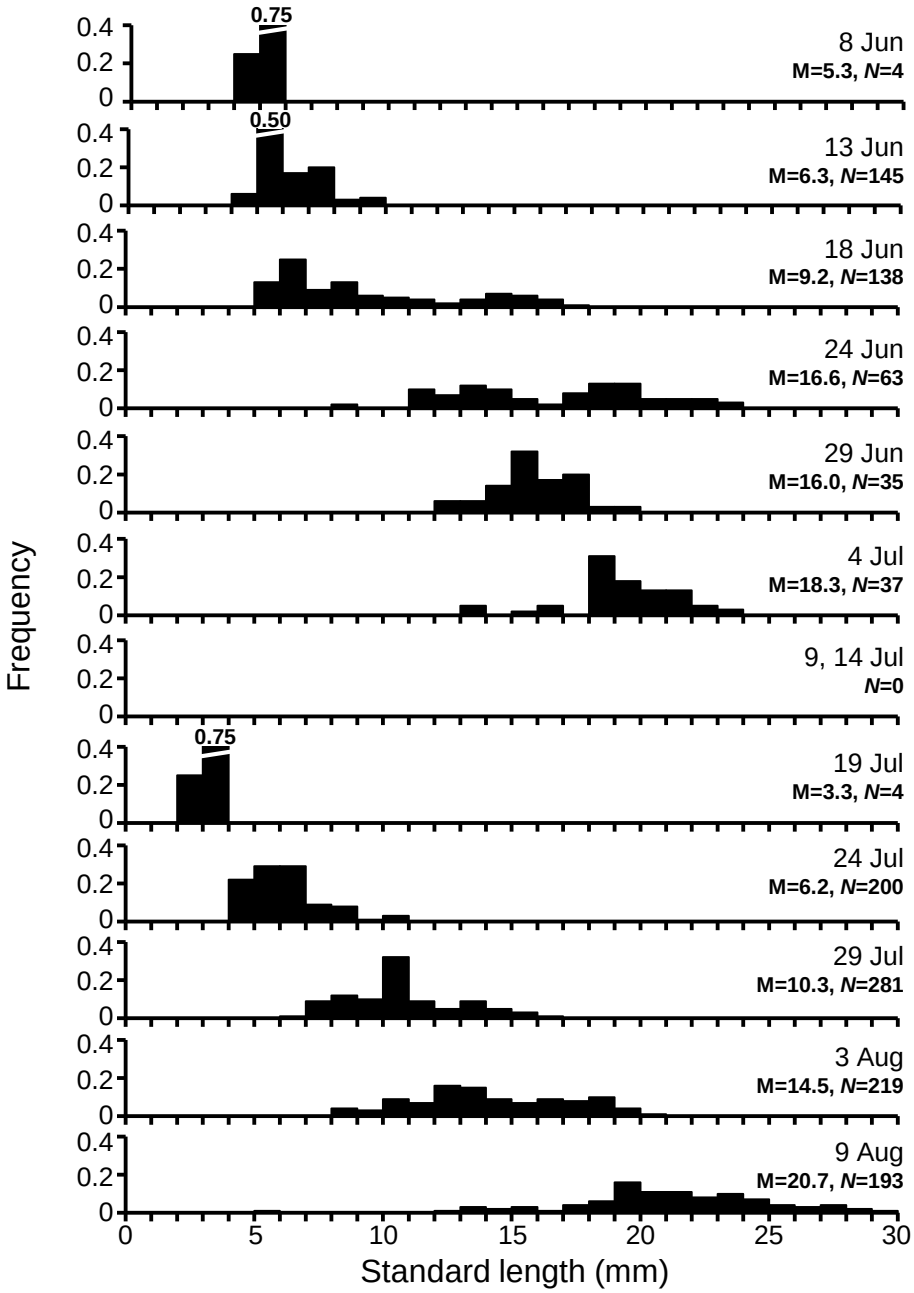

0.75
8 Jun
M=5.3, N=4
0.50
13 Jun
M=6.3, N=145
18 Jun
M=9.2, N=138
24 Jun
M=16.6, N=63
29 Jun
M=16.0, N=35
4 Jul
M=18.3, N=37
9, 14 Jul
N=0
0.75
19 Jul
M=3.3, N=4
24 Jul
M=6.2, N=200
29 Jul
M=10.3, N=281
3 Aug
M=14.5, N=219
9 Aug
M=20.7, N=193
Frequency
0.4
0.2
0
0
5
10
15
20
25
30
Standard length (mm)

Fig. 5

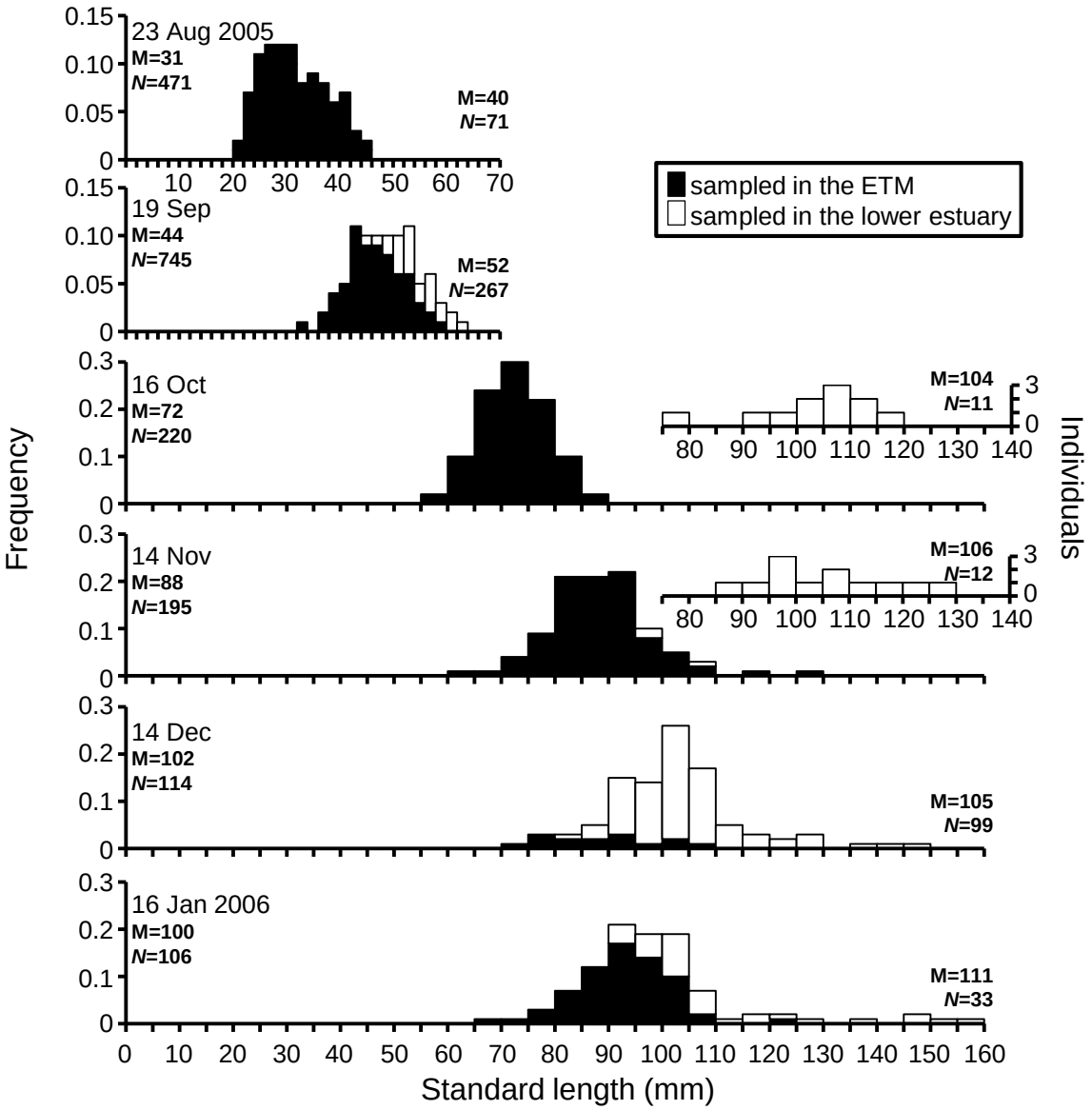

23 Aug 2005
M=31
N=471
M=40
N=71
19 Sep
M=44
N=745
M=52
N=267
16 Oct
M=72
N=220
M=104
N=11
14 Nov
M=88
N=195
M=106
N=12
14 Dec
M=102
N=114
M=105
N=99
16 Jan 2006
M=100
N=106
M=111
N=33
sampled in the ETM
sampled in the lower estuary
Frequency
Individuals
Standard length (mm)

Fig. 6

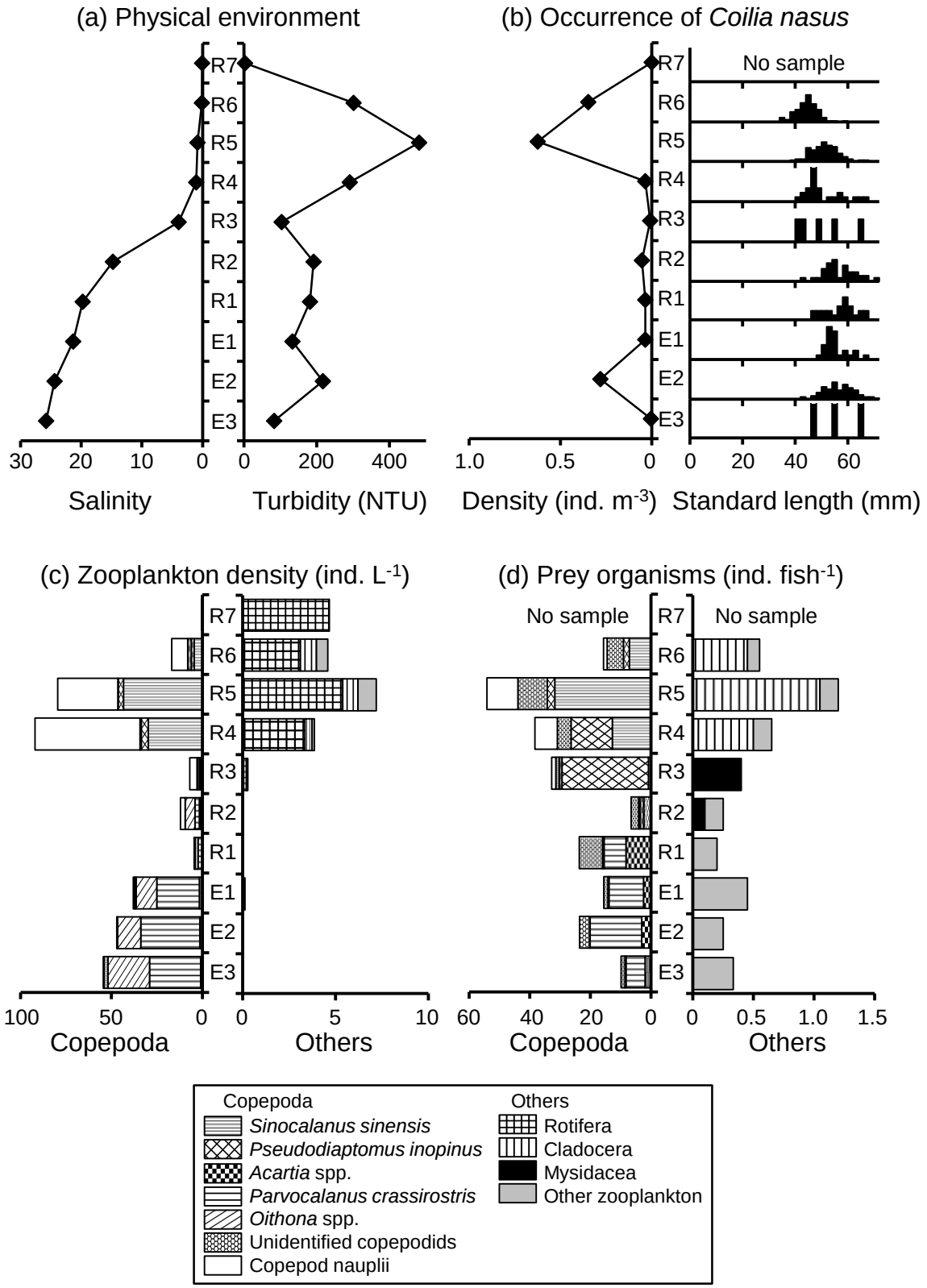

(a) Physical environment
(b) Occurrence of *Coilia nasus*
R7
R6
R5
R4
R3
R2
R1
E1
E2
E3
No sample
30 20 10 0
0 200 400
Salinity
Turbidity (NTU)
1.0 0.5 0
0 20 40 60
Density (ind. m-3)
Standard length (mm)
(c) Zooplankton density (ind. L-1)
(d) Prey organisms (ind. fish-1)
No sample
No sample
100 50 0
0 5 10
Copepoda
Others
60 40 20 0
0 0.5 1.0 1.5
Copepoda
Others
Copepoda
Sinocalanus sinensis
Pseudodiaptomus inopinus
Acartia spp.
Parvocalanus crassirostris
Oithona spp.
Unidentified copepodids
Copepod nauplii
Others
Rotifera
Cladocera
Mysidacea
Other zooplankton

Fig. 7

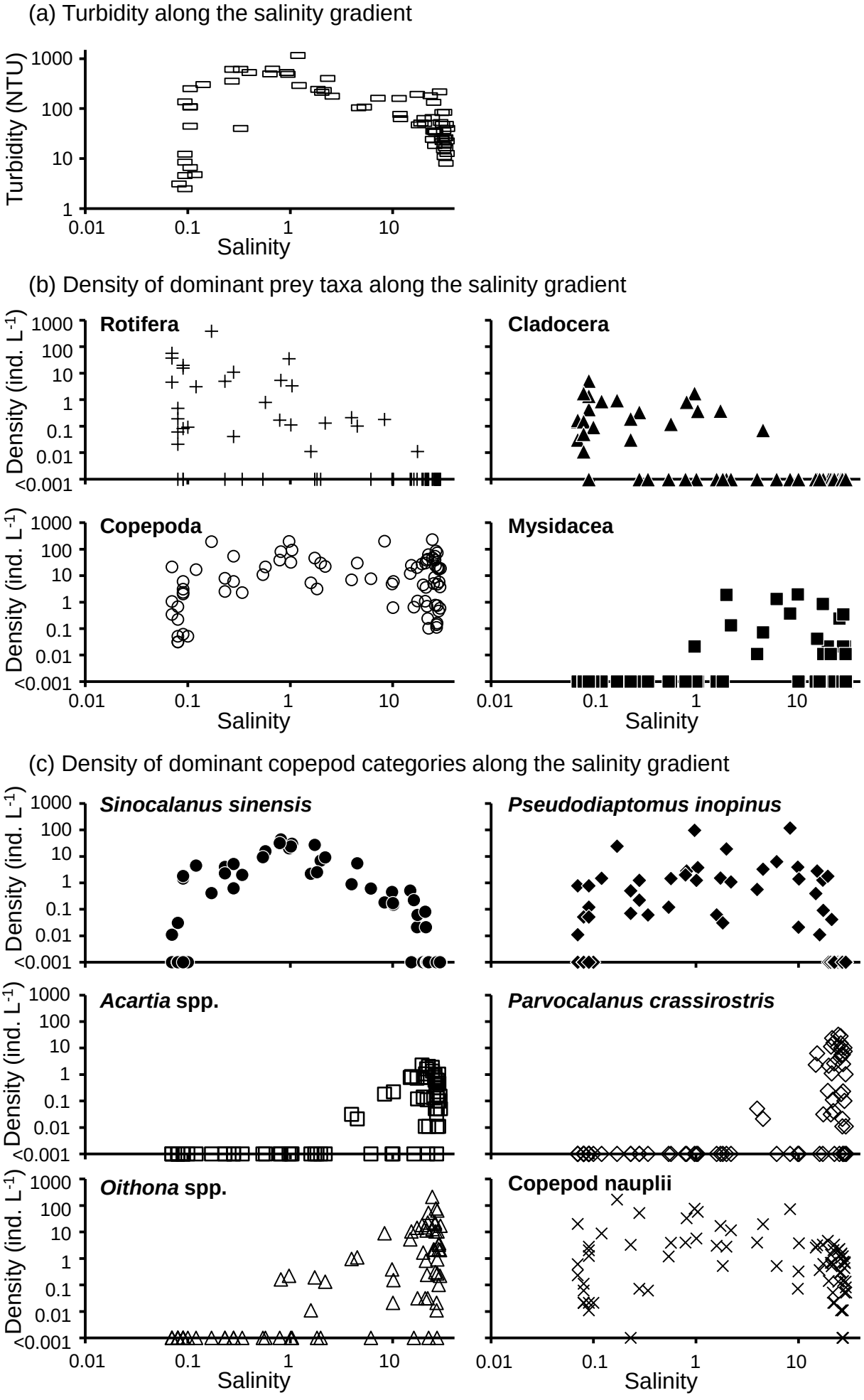

(a) Turbidity along the salinity gradient
Turbidity (NTU)
1000
100
10
1
0.01
0.1
1
10
Salinity
(b) Density of dominant prey taxa along the salinity gradient
Density (ind. L-1)
Rotifera
Cladocera
Copepoda
Mysidacea
1000
100
10
1
0.1
0.01
<0.001
0.01
0.1
1
10
Salinity
(c) Density of dominant copepod categories along the salinity gradient
Sinocalanus sinensis
Pseudodiaptomus inopinus
Acartia spp.
Parvocalanus crassirostris
Oithona spp.
Copepod nauplii

Fig. 8

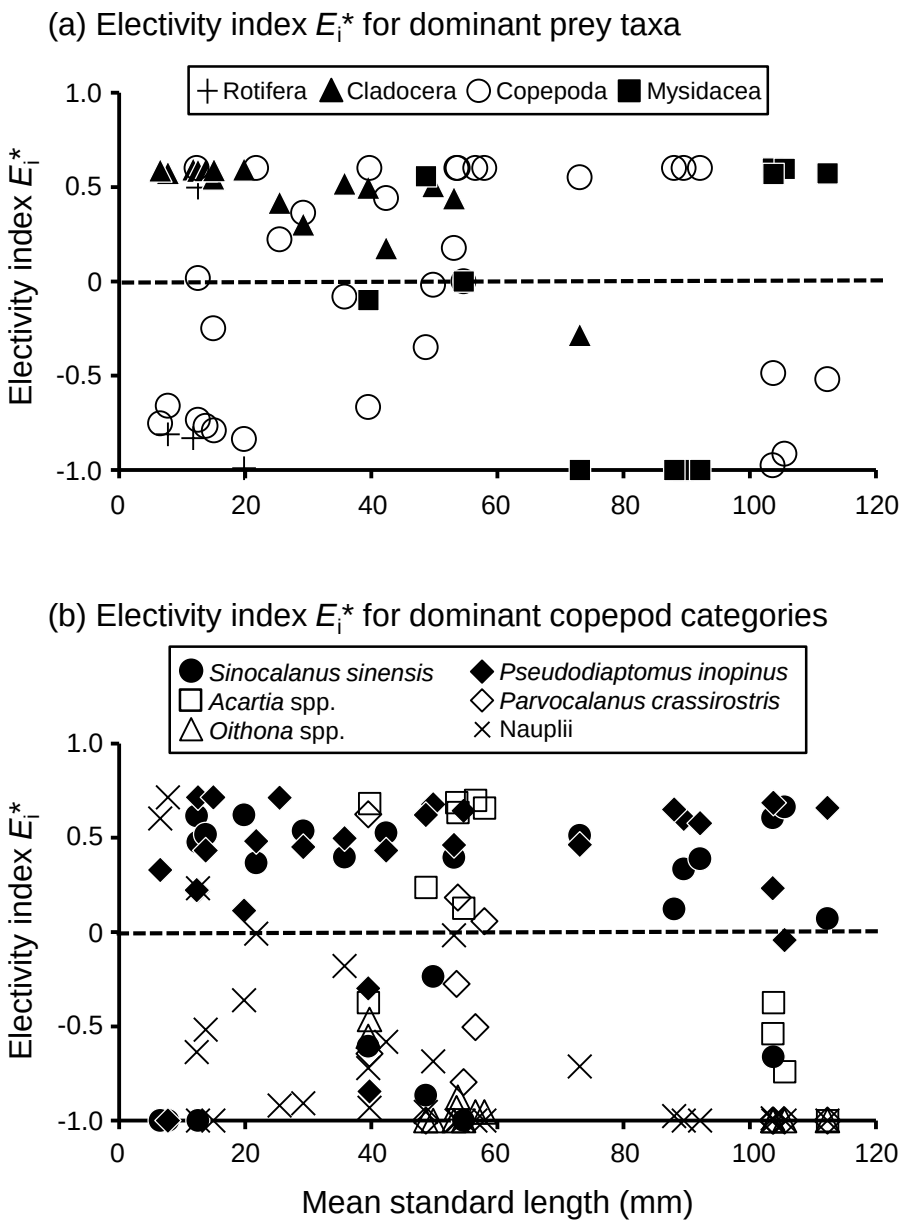

(a) Electivity index E_i* for dominant prey taxa
Rotifera
Cladocera
Copepoda
Mysidacea
Electivity index E_i*
1.0
0.5
0
-0.5
-1.0
0
20
40
60
80
100
120
(b) Electivity index E_i* for dominant copepod categories
Sinocalanus sinensis
Pseudodiaptomus inopinus
Acartia spp.
Parvocalanus crassirostris
Oithona spp.
Nauplii
Electivity index E_i*
Mean standard length (mm)

Fig. 9

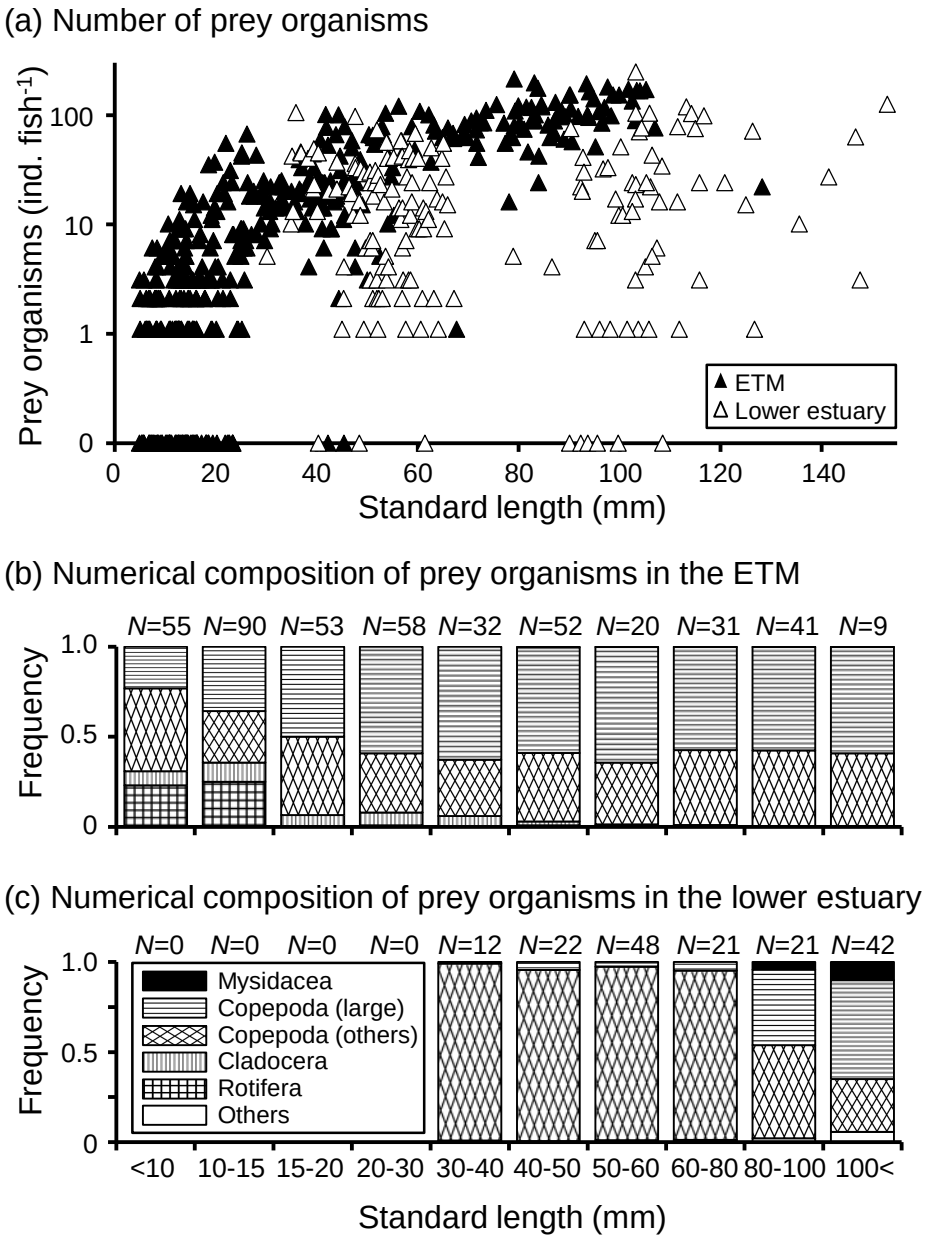

(a) Number of prey organisms
Prey organisms (ind. fish-1)
100
10
1
0
ETM
Lower estuary
0
20
40
60
80
100
120
140
Standard length (mm)
(b) Numerical composition of prey organisms in the ETM
N=55 N=90 N=53 N=58 N=32 N=52 N=20 N=31 N=41 N=9
Frequency
1.0
0.5
0
(c) Numerical composition of prey organisms in the lower estuary
N=0 N=0 N=0 N=0 N=12 N=22 N=48 N=21 N=21 N=42
Frequency
1.0
0.5
0
Mysidacea
Copepoda (large)
Copepoda (others)
Cladocera
Rotifera
Others
<10
10-15
15-20
20-30
30-40
40-50
50-60
60-80
80-100
100<
Standard length (mm)

Fig. 10

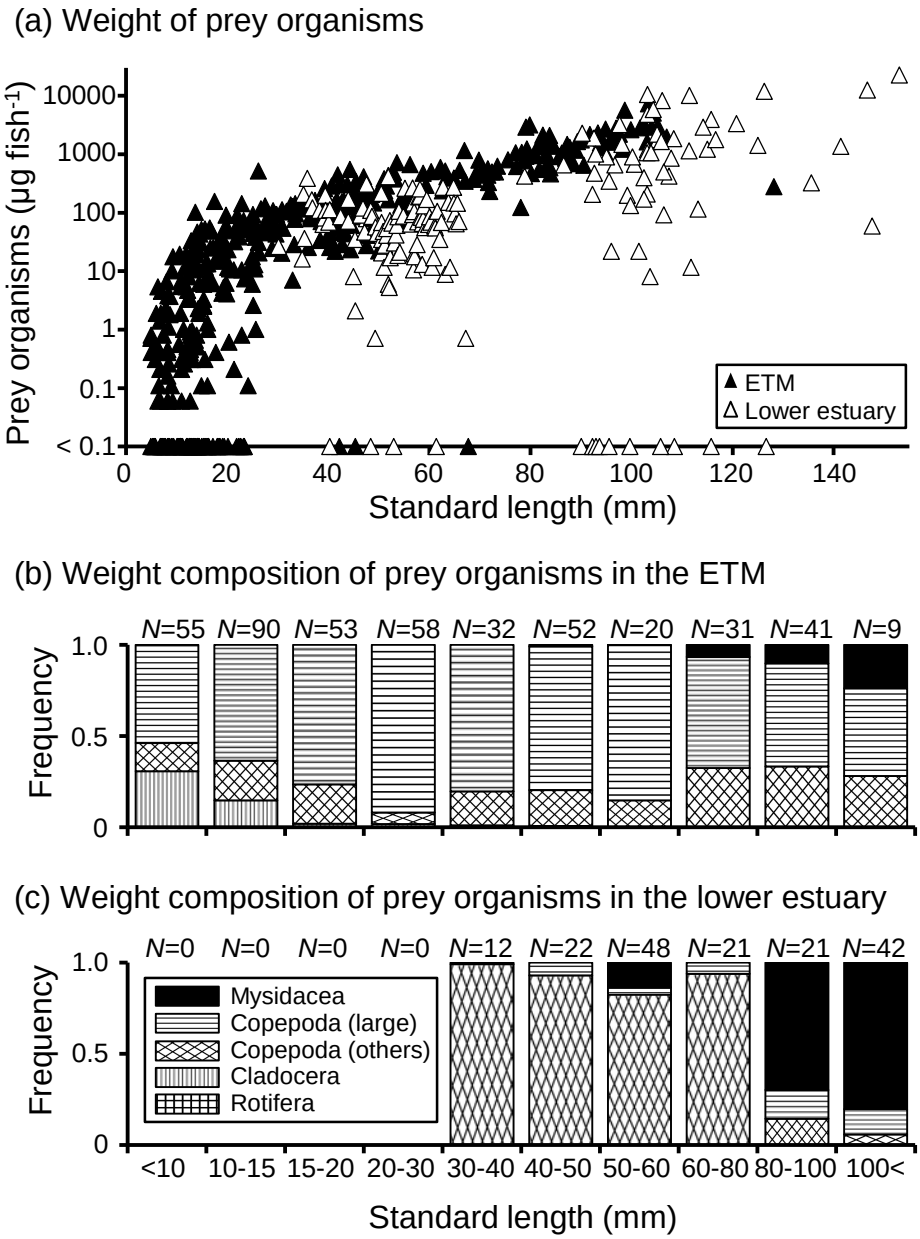
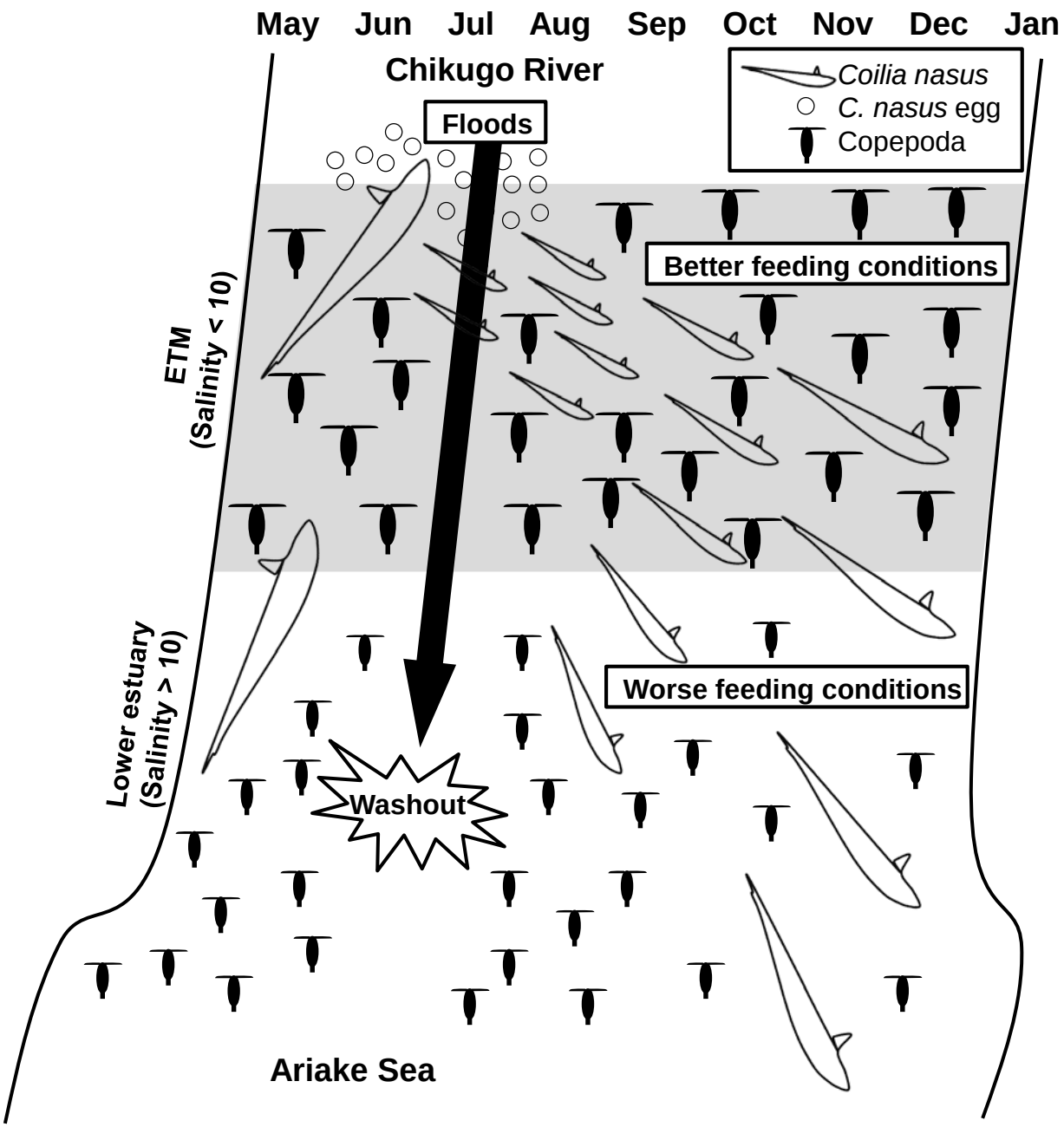

(a) Weight of prey organisms
Prey organisms (μg fish-1)
10000
1000
100
10
1
0.1
< 0.1
0
20
40
60
80
100
120
140
Standard length (mm)
ETM
Lower estuary
(b) Weight composition of prey organisms in the ETM
N=55 N=90 N=53 N=58 N=32 N=52 N=20 N=31 N=41 N=9
Frequency
1.0
0.5
0
(c) Weight composition of prey organisms in the lower estuary
N=0 N=0 N=0 N=0 N=12 N=22 N=48 N=21 N=21 N=42
Frequency
1.0
0.5
0
Mysidacea
Copepoda (large)
Copepoda (others)
Cladocera
Rotifera
<10
10-15
15-20
20-30
30-40
40-50
50-60
60-80
80-100
100<
Standard length (mm)

Fig. 11


May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Chikugo River
Floods
Coilia nasus
C. nasus egg
Copepoda
Better feeding conditions
ETM
(Salinity < 10)
Lower estuary
(Salinity > 10)
Worse feeding conditions
Washout
Ariake Sea